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Captive killer whale (*Orcinus orca*) survival

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Abstract

Killer whales (*Orcinus orca*) were first placed into captivity in 1961 and are now found in theme parks around the world. Despite successful breeding of captive killer whales since 1985 there is growing concern for their welfare in captivity, which often includes claims of poor survival. We employed Kaplan-Meier and Cox Proportional hazards models and annual survival rate analyses on 201 captive killer whales to discern how sex, facility (U.S. *vs*. foreign), captive-born *vs*. wild-captured, pre- *vs*. post-1 January 1985, and animal age upon entering captivity affect survival. Overall median survival estimate was 6.1 yr, with no difference between male and female survival. Killer whales in U.S. facilities (12.0 yr) demonstrated a significantly higher median survival than those in foreign facilities (4.4 yr), as did whales entering captivity post-1 January 1985 (11.8 yr) *vs.* those entering prior to 1 January 1985 (3.9 yr). Median survival for captive-born (14.1 yr) was significantly higher than wild-captured killer whales (5.5 yr), though the two failed to differ among the post-1 January 1985 cohort. Facility location and pre- *vs*. post-1 January 1985 were predictors of the hazard rate. Survival of captive killer whale cohorts has generally improved through time, although survival to age milestones are poor when compared to wild killer whales.

Key words: captive killer whale, *Orcinus orca*, Kaplan-Meier, Cox proportional hazard, annual survival rate.

Killer whales (*Orcinus orca*) were first placed into captivity in the United States (U.S.) in 1961. Since then their use in theme parks has spread to numerous countries although diverse health and other problems related to captivity have been reported (*e.g*., St. Leger *et al.* 2011, Jett and Ventre 2013). Growing concern for the welfare of captive killer whales is evidenced by a recent panel discussion in which survival and other health-related matters were prominent topics among marine mammal specialists[2]. The deaths of killer whale trainers in 1991,[3] 2009,[4] and 2010, and a park guest in 1999 by captive killer whales owned by a U.S.-based theme park (Parsons 2012) have served to generally heighten the scrutiny of keeping killer whales for entertainment purposes. Criticisms of the prac-

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[2]https://weforg.files.wordpress.com/2014/01/panelkwenglish.pdf.

[3]The whale, owned by a Canadian company at the time of the trainer's death in 1991, was subsequently sold to a U.S.-based theme park where it killed a park guest in 1999 and a trainer in 2010.

[4]The whale, owned by a U.S.-based theme park, killed a trainer while housed in a foreign theme park.

tice often focus on the negative health and psychological consequences of captivity, including claims of poor survival (*e.g.*, Dougherty 2013).

To address growing concern for captive animals in general, a developing body of literature has begun to focus on the evaluation of welfare among animals held in zoos, with some researchers suggesting that assessments of survival and mortality provide a useful approach (*e.g.*, Walker *et al.* 2012). Demonstrating the use of zoo animal survival, the number of inter-zoo transfers (Clubb *et al.* 2008, 2009) and early maternal separations (Clubb *et al.* 2009) were both found to predict increased mortality/poorer survival among captive elephants (*Elephas maximus and Loxodonta africana*). The authors also showed that wild-captured elephants enjoyed higher survival than those born in captivity. Similar research showed that black rhinoceros (*Diceros bicornis*) survival was negatively associated with the percentage of enclosure exposed to the public (Carlstead *et al.* 1999). Survival has also been evaluated within the context of subjective evaluations of well-being among captive orang-utans (*Pongo* spp.), with researchers noting higher survival among those animals judged by keepers as displaying higher rather than lower positive affect (Weiss *et al.* 2011).

Captive cetaceans in the U.S. are tracked and accounted for by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NOAA Fisheries) as mandated by the U.S. Marine Mammal Protection Act to maintain inventory of whales, dolphins, porpoises, and other marine mammals held for, among other purposes, public display.[5] Facilities displaying cetaceans, including those in foreign countries that send or receive animals from the U.S., are required to submit to NOAA details such as the name of their holding institution, the sex and age of the animal, date entering captivity (through wild-capture or birth), animal imports, disposition of the animal (death, transfer or release), and date upon death. Submitted data are contained within the Marine Mammal Inventory Report (MMIR) maintained by NOAA Fisheries. Whereas data contained in the MMIR are mostly limited to animals held in U.S. facilities, data on captive killer whales housed in foreign facilities have been compiled by The Orca Project (TOP)[6] to provide the same details as those contained in the MMIR.

Several studies have used the MMIR to evaluate annual survival rates (ASR) among captive marine mammals through time and/or among animals housed in various facilities (DeMaster and Drevenak 1988, Duffield and Miller 1988, Small and DeMaster 1995, Woodley *et al.* 1997). For example, using ASR analysis on killer whales held mostly in U.S.-based parks, Small and DeMaster (1995) found annual survival higher for females than males, although they detected no differences in survival among various institutions housing killer whales. They additionally compared annual survival of wild-captured and captive-born marine mammals of various species, though an absence of captive killer whale deaths at the time of their analyses hindered comparison between the two groups.

In 1985 an enlarged pool (completed in 1984) marked the beginning of improved captive killer whale breeding by enabling adequate nursing behavior between a mother and captive-born calf (Asper *et al.* 1988). Since that time, the proportion of captive-born to wild-captured killer whales has increased domestically and abroad. Despite the trend to supply parks with captive-born whales, one whale, captured in

[5]National Oceanic and Atmospheric Administration: http://www.nmfs.noaa.gov/pr/permits/inventory.htm. Accessed 20 November 2013.

[6]The Orca Project: http://theorcaproject.wordpress.com/killer-whale-orca-database/. Accessed 5 April 2014.

2012, now resides in a Russian park, and an additional seven killer whales were captured in the Sea of Okhotsk (Russia) as recently as 2013 for likely sale to a Chinese facility.[7] Although the general demographics of killer whales held in captive environments have changed since captivity began, there has been little research to evaluate survival within the context of these changes.

Therefore, the focus of this paper is twofold. First, a follow-up to Small and DeMaster's (1995) analyses using ASR will allow for general comparison to their research. Second, using Kaplan-Meier (KM) and Cox Proportional hazards models, evaluations of survival among sexes, among killer whales housed domestically and abroad, and among wild-captured and captive-born whales will provide for an evaluation of the differences in survival given these covariates, and how survival changes through time. The survival curves generated by the KM analyses should inform management practices and surveillance of captive animal health during periods when survival is shown to improve or deteriorate, given a particular animal cohort. Similarly, as some countries housing killer whales have little to no regulation of zoological parks (Cooper 2003), an examination of survival and hazard ratios and comparisons of these metrics between foreign and U.S. facilities may help to guide standards of care provided in these facilities.

Materials and Methods

Data from the MMIR and TOP were analyzed with SPSS (v. 21; IBM 2013) and G*Power (v. 3.1.9.2; Faul *et al.* 2007). We employed the KM survival estimate, Cox proportional hazards regression, and ASR to evaluate the following research questions based on captive killer whales:

1. What is the overall survival estimate?
2. Are there differences in survival estimates between sexes?
3. Are there differences in survival estimates between U.S. and foreign facilities?
4. Are there differences in survival estimates between captive-born and wild-captured killer whales?
5. Are there differences in survival estimates prior to, and post-1 January 1985?
6. How has survival changed through time?
7. How do the following covariates influence the captive killer whale hazard rate:
   a. Sex
   b. Facility location
   c. Captive-born/wild-captured
   d. Pre- *vs*. post-1 January 1985
   e. Animal age upon entering captivity

Duration of captivity (DOC) (in days; later converted to years) was calculated from the day an animal was placed or born into captivity until the day it died. In cases where an animal was still alive (*i.e.*, "censored") at the time this research was conducted we used 1 January 2014 to calculate DOC. We also coded for sex, location of facility (U.S. or foreign), captive-born or wild-captured, and pre- or post-1 January

[7]Far East Russia Orca Project: http://russianorca.com/index.php?lang=en. Accessed 19 November 2014.

1985. Age upon entering captivity estimates were also entered; mean age estimates were imputed for the four animals for which no estimates were available. Recent Russian captures were excluded from analyses.

We calculated KM survival estimates for all animals recorded in the MMIR and TOP (18 November 1961–1 January 2014), which allowed for the computing of probabilities of experiencing death given those animals that had died, as well as those animals still alive at the study's conclusion (Nuss and Warneke 2010). The KM analyses generated survival statistics based on the number of animals at risk and the number of animals who either died (*i.e.*, positive for an event) or who were still alive at the end of the study (*i.e.*, "censored" observations; negative for an event) (Hosmer and Lemeshow 1999). Animals entered the analysis at various times (births and captures), thus we employed the staggered entry design (Pollock *et al.* 1989). In addition to generating overall estimates of survival and survival curves of individual cohorts, we employed the Mantel-Cox log-rank analysis at the 0.05 level of significance to test the null hypothesis of no survival differences between sexes, between animals housed in U.S. and foreign facilities, between captive-born and wild-captured animals, and between animals entering captivity before and after 1 January 1985. As mean survival time estimation cannot be reliably established with censored data for which no event has occurred, we cite median survival as the most appropriate descriptive statistic with KM analyses (Rao and Schoenfeld 2007, Gong and Fang 2012). Thus, we calculated median survival estimates, 25% and 75% survival quartile estimates, and 95% confidence intervals for each estimate. Additionally, the survival curves generated by the KM survival model provided graphical representation of the proportion of a cohort surviving ($S[t]$) at time t.

Like KM, the Cox proportional hazards model has demonstrated widespread utility in diverse disciplines including the medical (*e.g.*, Cuthbert *et al.* 2014) and wildlife fields (*e.g.*, Brzeski *et al.* 2014) due in part to its ability to manage right-censored survival data. As a regression model, the Cox approach allowed for an examination of the contribution of covariates to the hazards ratio, defined as the ratio of the rates of hazard between two or more groups of subjects (Spotswood *et al.* 2004). Thus, to better understand how sex, location of facility (U.S. *vs.* foreign), captive-born *vs.* wild captured, pre- *vs.* post-1 January 1985, and animal age upon entering captivity contributed to the hazard ratio we used the Cox model to nonparametrically model the hazard function based on survival of individual killer whales (Hosmer *et al.* 2008).

We tested individual covariates within the multivariate model at the 0.05 level of significance, and based on the results we then tested for interaction effects. The hazard ratio is reported to better understand how the variables in the model influence the chance that a death will occur. For example, a hazard ratio of "2" suggests that for an animal that has not died by a certain time, that animal has twice the chance of dying by the next point in time when compared to an animal belonging to a different group (Spotswood *et al.* 2004). Significant hazard ratios were converted to the odds of death occurring given each covariate, by the equation: odds = $HR/(1 + HR)$ (Spotswood *et al.* 2004). Thus, a hazard ratio of "2" represents a 67% chance that an animal from one group will die before an animal from another group.

Additionally, using the approach of DeMaster and Drevenak (1988), Small and DeMaster (1995) and others, we generated ASRs by first determining daily survival rates (calculated as 1 – [# animal deaths/# total animal days]) and then annual survival rates (calculated as daily survival rate raised to the 365.25 power) for whales within each cohort evaluated. Confidence intervals were calculated based upon the standard error for the binomial distribution (Steel *et al.* 1997), which included daily survival

rate, daily mortality rate and number of animal days in each cohort. In addition to generating ASR and 95% confidence intervals within cohorts, we employed the Mann-Whitney U test at the 0.05 level of significance to test the null hypothesis of no differences in ASR between the sexes, between animals housed in U.S. and foreign facilities, between captive-born and wild-captured animals, and between animals entering captivity before and after 1 January 1985.

Results

Data for 201 captive killer whales were examined. Captive-born animals totaled 66 (33%), whereas 135 were wild-captures (67%) (Fig. 1). One hundred eight (80%) of the 135 wild whales were captured prior to 1985. Of the 201 captive whales analyzed, 109 (54%) were female, and 92 (46%) were male (Table 1). One hundred twelve animals entered captivity prior to 1 January 1985 (56%); 89 (42%) entered captivity post-1 January 1985. In total, 18 of 66 (27%) captive-born killer whales died within the first six months of life. Four captive-born killer whales were born prior to 1 January 1985 (6%), of which none lived longer than two months. Sixty two (94%) captive-born calves were born post-1 January 1985, of which 12 (19%) lived fewer than six months. The estimated mean age of female and male wild-captured whales entering captivity was 5.44 yr and 5.04 yr, respectively.

Eighty three (41%) were housed in U.S. facilities, whereas 118 (59%) were kept in one of at least 15 foreign countries having housed killer whales since the practice began. In total, 154 (77%) captive whales had died by 1 January 2014, and of those that have died, 97 (63%) died prior to their sixth year of captivity; 132 (86%) whales

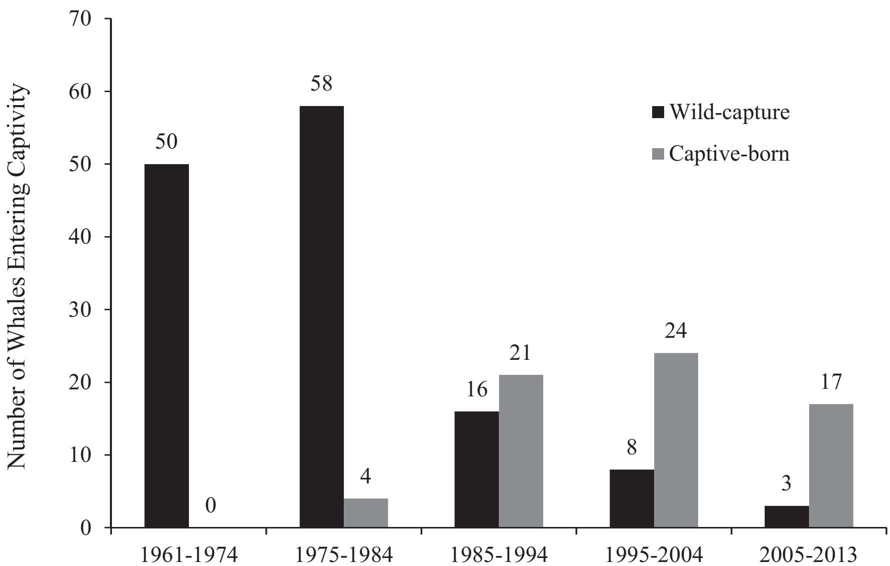

Figure 1. Distribution of captive-born *vs.* wild-captured *O. orca* from 1961 to 31 December 2013. The values embedded in the graph represent the total number of animals who entered captivity, either through wild-capture or captive-birth, for each time category. One whale entered captivity in 1961, hence the expanded time interval, 1961–1974.

Table 1. Distribution of captive-born and wild-captured *O. orca* from 1961 to 31 December 2013. Values depict the total number of whales of each sex, facility (whether U.S. or foreign), and whether pre- or post-1 January 1985. Mean age upon entering captivity is 0 yr for captive-born and 5.4 yr and 5.0 yr for wild-captured females and males, respectively.

		Male	Female	Total
U.S.	Pre-1 January 1985			
	Captive-born	2	1	3
	Wild-capture	21	29	50
	Post-1 January 1985			
	Captive-born	9	21	30
	Wild-capture	0	0	0
Foreign	Pre-1 January 1985			
	Captive-born	1	0	1
	Wild-capture	33	25	58
	Post-1 January 1985			
	Captive-born	16	16	32
	Wild-capture	10	17	27
Total		92	109	201

died prior to their 16th year of captivity (Fig. 2). Of the 48 captive killer whales alive as of 1 January 2014, eight (17%) had lived beyond their 30th year of captivity (4% of the 201 whales examined).

Overall, Male and Female, and U.S. and Foreign Survival

The overall KM median survival estimate was 6.1 yr (95% CI: 2.7–9.4 yr) (Fig. 3a). The overall survival curve demonstrates a steep initial decline in survival upon entering captivity, which begins to improve slightly at 0.7 yr. An abrupt decline in survival occurs at 2.2 yr, and an improvement in survival appears at 6.2 yr and again at 12.0 yr. Survival deteriorates again between 19.2 yr and 21.2 yr. Approximately 25% of whales survived 19.3 yr (Table 2), with an overall ASR of 0.917 (95% CI: 0.905-0.930) (Table 3). A linear trend line of overall ASR (y = 0.022x + 0.763; R^2 = 0.625) demonstrates general improvement in survival through time, with ASR improving an average of 5.3% every 5 yr.

Kaplan-Meier survival curves for each sex are shown in Figure 3b. Overall median survival estimate for females was 9.6 yr (95% CI: 4.8–14.4 yr) and 5.1 yr (95% CI: 3.2–6.9 yr) for males. Employing the Mantel-Cox log rank test, survival estimates between sexes were not significantly different (χ^2 = 1.165, P = 0.280), although the ability to detect a difference was rather low (1 – β = 0.38). Male and female survival curves both show an initial steep decline in survival and remain overlapped until 3.0 yr, at which time female and male survival diverge, with females experiencing higher survival throughout the remainder of the distribution. Survival deteriorates for females between 7.0 yr and 11.0 yr while improving for males during this period. Survival declines more rapidly for males than females between 2.7 yr and 6.0 yr at which point survival for both improves. The survival curves remain somewhat parallel beyond the 2.7 yr point, although females appear to experience marked decline in survival at 10.0 yr, and improvement from 15.0 yr to 18.5 yr before demonstrating

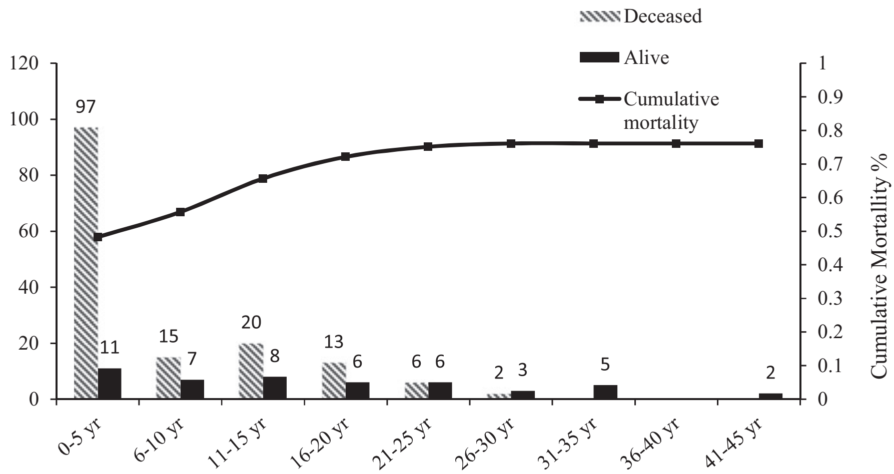

Figure 2. Distribution of the total number of captive *O. orca* within each duration of captivity category, including both those who have died within each category and those still alive as of 31 December 2013. The values embedded in the graph represent the total number of whales represented in the MMIR who lived and died in each category after entering captivity; cumulative mortality is represented by the line.

a steep decline in survival between 18.5 yr and 21.0 yr. Approximately 25% of males and females survived to 15.7 yr and 20.0 yr, respectively. Overall ASR for females (0.926; 95% CI: 0.911–0.942) and males (0.904; 95% CI: 0.883–0.925) did not differ significantly (Z = –0.238, P = 0.709), although again, the ability to detect a difference was limited ($1 - \beta = 0.21$). Linear trend lines for both female ($y = 0.023x + 0.760$; $R^2 = 0.485$) and male ($y = 0.021x + 0.760$, $R^2 = 0.587$) ASRs demonstrate general improvement in survival through time, with ASR improving an average of 5.2% and 4.1% every five yr for female and males, respectively.

Kaplan-Meier survival curves for whales held in U.S. and foreign facilities are shown in Figure 3c. The median survival between whales housed in U.S. facilities and foreign facilities (12.1 yr; 95% CI: 8.5–15.5 yr) and (4.3 yr; 95% CI: 2.6–5.9 yr) respectively, was significantly different ($\chi^2 = 6.53$; $P = 0.01$). After stratifying pre- and post-1 January 1985 (analysis below), the difference between survival estimates of whales housed in the U.S. *vs*. those held in foreign facilities continued to differ significantly ($\chi^2 = 8.99$; $P = 0.003$). Similarly, after stratifying wild-capture and captive-born whales, the difference between survival estimates of whales housed in the U.S. *vs*. those held in foreign facilities continued to differ significantly ($\chi^2 = 4.780$, $P = 0.027$). Survival curves demonstrate a separation in survival almost immediately upon entering captivity, with survival of whales housed in U.S. facilities higher than those in foreign facilities. Survival of whales in U.S. facilities appears to improve somewhat at about 1.0 yr and again at approximately 6.0 yr, but a marked decline in survival (U.S.) is seen at 10.0 yr and again at 12.0 yr, at which point the slope of the line indicates similar or poorer survival than whales held in foreign facilities until about 21.1 yr. Approximately 25% of U.S.-housed whales and foreign-housed whales survived to 20.9 yr and 14.9 yr, respectively. Overall ASR among U.S. (0.939; 95% CI: 0.924–0.954) and foreign-housed whales (0.893; 95% CI:

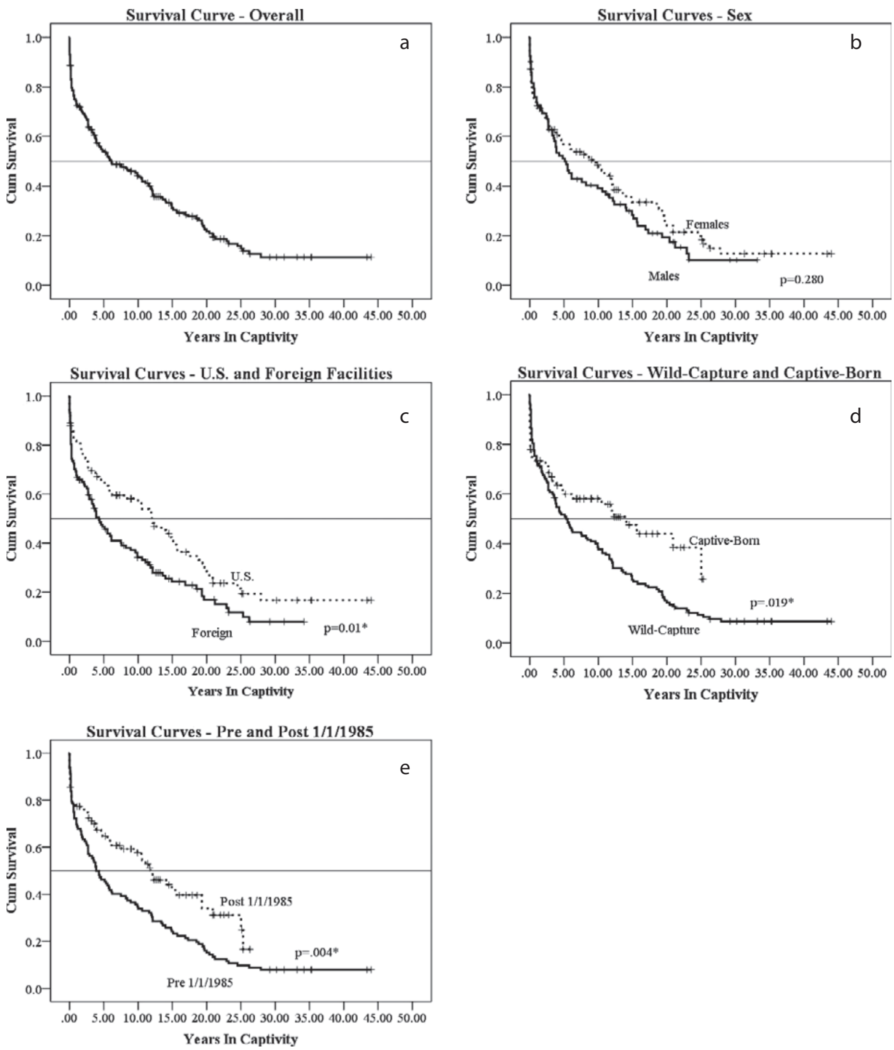

Figure 3. Kaplan-Meier survival curves representing the proportion of *O. orca* alive over time for all whales (a), each sex (b), U.S. and foreign facilities (c), wild-captures and captive-born whales (d), and pre- and post-1 January 1985 (e). The horizontal line depicts 50% survival; significant *P*-values are shown with an asterisk. Tick marks on each curve indicate a specific censored animal, with some ticks overlapping each other.

0.873–0.914) did not differ significantly ($Z = -1.659$, $P = 0.094$) but the ability to detect a difference was somewhat limited ($1 - \beta = 0.29$). Linear trend lines of both U.S. ($y = 0.019x + 0.809$, $R^2 = 0.609$) and foreign ($y = 0.032x + 0.664$, $R^2 = 0.605$) ASRs demonstrate general improvement through time, with ASR improving 3.7% and 7.8%, on average, every five yr for whales held in U.S. and foreign facilities, respectively.

Table 2. Quartiles of the Kaplan-Meier survival estimates for captive *O. orca*. Values under percentiles are years surviving in captivity as represented by the survival curves. Note that cumulative survival for captive-born whales has yet to fall below 25%.

	KM survival estimates		
	25%	50%	75%
Overall	19.3	6.1	0.7
Male	15.7	5.1	1
Female	20	9.6	0.6
U.S.	20.9	12	2
Foreign	14.9	4.4	0.3
Wild-Captured	15	5.5	1
Captive-Born	na	14.1	0.3
Pre-1 January 1985	14.8	3.9	0.6
Post-1 January 1985	25	11.8	2.3

Wild-Captured and Captive-Born, and Pre- and Post-1 January 1985 Survival

Kaplan-Meier survival curves for wild-captured and captive-born whales are depicted in Figure 3d. The difference in median survival between whales captured from the wild and captive-born whales, (5.5 yr; 95% CI: 3.7–7.3 yr) and (14.1 yr; 95% CI: 8.1–20.0 yr), respectively, was significantly different (χ^2 = 5.46, P = 0.019). The survival estimates between wild-captured and captive-born animals within the post-1 January 1985 cohort failed to differ significantly (χ^2 = 0.735, P = 0.391), but the ability to detect a difference was somewhat limited ($1 - \beta = 0.30$). Survival curves demonstrate a steep initial decline in survival for both wild-captured and captive-born whales. Survival among wild-captured whales is smooth, with an improvement in survival at 6.0 yr and 12.0 yr. Survival among captive-born whales shows improvement in survival at approximately 1.0 yr of age at which point survival improves until 2.0 yr where it then declines until 6.0 yr. Captive-born survival improves again at 15.5 yr. Approximately 25% of wild-captured whales survived to 15.1 yr; cumulative survival for captive-born whales remains just above 25%. Overall ASR among wild-captured (0.908; 95% CI: 0.893–0.924) and captive-born whales (0.938; 95% CI: 0.918–0.958) failed to differ ($Z = -0.788$, $P = 0.392$) and the ability to detect a difference was somewhat improved over prior analyses ($1 - \beta = 0.48$). The linear trend line of wild-captured whale ASRs ($y = 0.017x + 0.794$, $R^2 = 0.491$) demonstrate general improvement through time, with ASRs having improved 3.7%, on average, every 5 yr (0.52%, on average, every 5 yr between 1994 and 31 December 2013). The linear trend line of captive-born whale ASRs ($y = 0.009x + 0.929$, R^2 = 0.3019) between 1994 and 31 December 2013 demonstrates general improvement over time, with ASRs having improved 1.3%, on average, every 5 yr. A comparison of captive-born and wild-capture ASRs during the entire history of captivity was not possible as there were no whales born in captivity between 1961 and 1973, and all captive-born whales died in the 1974–1983 interval.

Kaplan-Meier survival curves for both pre- and post-1 January 1985 are shown in Figure 3e. The difference in median survival between whales entering captivity prior to 1 January 1985 and whales entering captivity post-1 January 1985, (3.9 yr; 95% CI: 2.1–5.6 yr) and (11.8 yr; 95% CI: 8.3–15.2 yr), respectively, was significant (χ^2 = 8.151, P = 0.004), although survival during the two periods failed to differ once age upon arrival estimates were added to both cohorts (χ^2 = 0.831, P = 0.361).

Table 3. Annual survival rates of captive *O. orca* for each factor. Values in parentheses represent 95% confidence intervals. One whale entered captivity in 1961, hence the expanded time interval, 1961–1968.

	Annual survival rates						
Interval	Total	Female	Male	U.S.	Foreign	Wild–capture	Captive–born
1961–1968	0.671 (0.509–0.885)	0.628 (0.418–0.944)	0.725 (0.504–0.999)	0.720 (0.540–0.960)	0.537 (0.266–0.999)	0.705 (0.527–0.890)	na
1969–1973	0.872 (0.817–0.933)	0.806 (0.701–0.928)	0.912 (0.852–0.976)	0.908 (0.846–0.975)	0.818 (0.718–0.933)	0.872 (0.826–0.937)	na
1974–1978	0.855 (0.795–0.922)	0.944 (0.885–0.999)	0.781 (0.687–0.889)	0.877 (0.809–0.951)	0.808 (0.691–0.946)	0.873 (0.816–0.935)	0.000
1979–1983	0.842 (0.791–0.896)	0.894 (0.837–0.955)	0.773 (0.687–0.871)	0.919 (0.867–0.974)	0.753 (0.667–0.850)	0.857 (0.796–0.901)	0.000
1984–1988	0.925 (0.892–0.961)	0.922 (0.879–0.967)	0.932 (0.877–0.991)	0.949 (0.910–0.990)	0.897 (0.840–0.960)	0.943 (0.912–0.975)	0.363 (0.134–0.979)
1989–1993	0.939 (0.909–0.971)	0.962 (0.932–0.992)	0.887 (0.816–0.964)	0.950 (0.912–0.990)	0.928 (0.881–0.977)	0.943 (0.910–0.976)	0.922 (0.842–0.999)
1994–1998	0.928 (0.896–0.961)	0.919 (0.878–0.971)	0.944 (0.898–0.993)	0.941 (0.899–0.984)	0.916 (0.870–0.965)	0.929 (0.891–0.969)	0.926 (0.870–0.985)
1999–2003	0.955 (0.930–0.980)	0.942 (0.907–0.962)	0.974 (0.946–0.999)	0.956 (0.920–0.995)	0.955 (0.923–0.988)	0.940 (0.902–0.979)	0.974 (0.946–0.999)
2004–2008	0.916 (0.883–0.950)	0.924 (0.884–0.966)	0.903 (0.848–0.962)	0.974 (0.943–0.999)	0.870 (0.817–0.926)	0.877 (0.816–0.942)	0.943 (0.907–0.980)
2009–2013	0.965 (0.942–0.989)	0.955 (0.922–0.991)	0.978 (0.950–0.999)	0.974 (0.947–0.999)	0.955 (0.913–0.994)	0.957 (0.905–0.999)	0.968 (0.936–0.996)
Overall	0.917 (0.905–0.930)	0.926 (0.911–0.942)	0.904 (0.883–0.925)	0.939 (0.924–0.954)	0.893 (0.873–0.914)	0.908 (0.893–0.924)	0.938 (0.918–0.958)

Survival curves show a steep initial decline in survival for whales entering captivity both prior to and beyond 1 January 1985. The survival curve of whales entering captivity prior to 1 January 1985 is smooth with no abrupt changes, although survival appears to improve slightly at 6.0 yr and again at 10.0 yr. The survival curve of post-1 January 1985 whales shows improvements at 1.0 yr and 6.0 yr, and general decline between 2.0 yr and 6.0 yr. Among post-1 January 1985 whales, survival appears to enter a period of steep decline at 10.0 yr until 12.5 yr. Beyond 12.5 yr, post-1 January 1985 whales experience abrupt survival improvements at 16.0 yr and 21.0 yr. Approximately 25% of pre-1 January 1985 and post-1 January 1985 whales survived to 14.8 yr and 25.0 yr, respectively. Overall ASR among pre-1 January 1985 (0.855; 95% CI: 0.824–0.887) and post-1 January 1985 (0.938; 95% CI: 0.926–0.951) did not differ ($Z = -1.659$, $P = 0.08.1$); the ability to detect a difference was moderate ($1 - \beta = 0.77$). Linear trend lines of both pre-1 January 1985 ($y = 0.057x + 0.670$, $R^2 = 0.694$) and post-1 January 1985 ($y = 0.004x + 0.922$, $R^2 = 0.201$) ASRs demonstrate general improvement over time. ASR has improved 10.5% and 0.9%, on average, every 5 yr for pre- and post-1 January 1985, respectively.

Cox Proportional Hazards Regression

We first evaluated the assumption of proportional hazards by visually examining the log scale of the survival curves between the dichotomous independent variables (Kleinbaum 1996), with curves demonstrating no violation of the assumption. All covariates (age upon entry, sex, wild/captive-born, pre/post-1 January 1985, and U.S./foreign) were then entered into the model with the results suggesting the model was a good fit to the data ($\chi^2 = 25.12$, $P = <0.000$). We then used a conditional stepwise approach with probability for predictor entry set at 0.05 and for predictor removal set at 0.10. Results of the stepwise analysis indicated that animal age upon entry ($P = 0.014$; hazard ratio = 1.064; 95% CI of hazard ratio: 1.01–1.12), facility location (U.S. *vs*. foreign) ($P = 0.008$; hazard ratio = 1.59; 95% CI of hazard ratio: 1.13–2.25), and pre- *vs*. post-1 January 1985 ($P = 0.036$; hazard ratio = 1.56; 95% CI of hazard ratio: 1.33–1.97) were significant predictors of the hazard rate. The interaction effects between age of entry and facility location and age of entry and pre/post-1 January 1985 were not significant.

Holding other covariates constant, each additional year of age upon entering captivity represents a 6.4% increase in the hazard ratio and a 52% higher chance of death on any given day once captivity begins. With other covariates held constant, killer whales held in foreign facilities face a 59% higher hazard ratio and a 61% higher chance of death on any given day than for those held in U.S. facilities. Similarly, killer whales entering facilities prior to 1 January 1985 face a 56% higher hazard ratio and a 60% higher chance of death on any given day than those entering facilities after 1 January 1985.

Discussion

Employing the KM survival analysis, the overall median survival estimate over the 53 yr history of killer whale captivity was 6.1 yr, with an overall ASR of 0.917. In comparison to Small and DeMaster's (1995) ASR values among noncalf captive killer whales housed in various U.S. institutions through 1992, we found that ASR among U.S. institutions had improved somewhat between 1994 and 31 December 2013

(0.937 *vs.* 0.961, respectively), though still lower than ASR reported for wild, noncalf killer whales (0.976) (Olesiuk *et al.* 1990). While survival is generally improved in both the post-1 January 1985 and captive-born cohorts when compared to pre-1 January 1985 and wild-captured whales, survival to age milestones is remarkably poorer for captive killer whales than for wild whales. For example, among wild female killer whales, 62%–81% are reported to reach the approximate age of 15 yr, and 41%–75% reach the approximate age of 40 yr (Olesiuk *et al.* 1990, 2005). Among the deceased captive killer whales we evaluated, 22 (27%) females lived to 15 yr (or longer) while three (4%) lived longer than 28 yr, once age upon arrival estimates were added. Similarly, among captive females still alive, 13 (46%) and two (7%) had reached the age of 15 yr (or longer) and 40 yr (or longer), respectively, once age upon arrival estimates were added. Further, while we employed the conventional and statistically more appropriate approach of citing median survival estimates throughout our KM analyses, the overall mean KM survival estimates were 16.3 yr and 13.1 yr for captive females and males, respectively, with age upon arrival estimates included. When compared to the proportions of wild whales reaching age milestones and mean life expectancy estimates among wild females (46.0 yr) and wild males (31.0 yr) (Olesiuk *et al.* 2005), captive killer whale survival is, thus far, dissimilar.

Past research on both wild (*e.g.* Olesiuk *et al.* 1990, 2005), and captive killer whales (*e.g.*, Small and DeMaster 1995), has noted that females likely exhibit higher survival than males. However, Olesiuk *et al.* (1990, 2005) did not test for differences between sexes, and Small and DeMaster (1995) noted that ASR values for females were not different in their study due to low power to detect a difference. Small and DeMaster's (1995) study employed data through 1992 and since that time an increasing number of killer whales have entered captivity through captive breeding. Most captive births (94%) occurred after 1 January 1985, secondary to enlarged pool designs first implemented by a U.S. facility in 1984 (Asper *et al.* 1988). Further fostering this growth, captive females are routinely impregnated by artificial means (Robeck *et al.* 2004). Although in our study, female and male survival failed to differ statistically, future research should more closely examine the potential survival implications of artificially impregnating young captive females.

The proportion of captive-born to wild-captured killer whales is generally increasing, although median survival between captive-born and wild-captured killer whales did not differ among the post-1 January 1985 cohort. Captive-born killer whales are, in general, younger than wild-captured whales in the post-1 January 1985 cohort, thus more research is necessary to better understand the interaction in the post-1 January 1985 cohort between age and captive-born *vs.* wild-capture. In our study, 16 of 33 (48%) deceased captive-born killer whales had died within the first six months of life; however, 74% of all captive-born calves (dead and alive) had survived the first six months. Bain (1990) and Olesiuk *et al.* (1990) reported that wild calf mortality may be as high as 37%–50% within the initial 6 mo of life, though Olesiuk *et al.* (2005) later suggested this figure may be an overestimate. Thus it appears that captive-born calf mortality within the first 6 mo is generally consistent with observations of wild killer whale calf mortality.

The overall median survival for whales held in U.S. facilities (12.0 yr) differed significantly from the overall median survival of those held in foreign facilities (4.4 yr), a finding generally corroborated by our ASR results (0.939 and 0.893) for U.S. and foreign facilities, respectively. Survival was found to be consistently higher for whales housed in U.S. facilities; however, survival in both foreign and U.S. facilities has failed to improve appreciably since 2003. Interestingly, the KM survival curves

demonstrate a decline in survival at approximately 10.0 yr and then again at 14.0 yr in captivity among whales in U.S. facilities, while survival improves slightly at these time points for whales in foreign facilities. Despite this, survival curves for U.S. and foreign facilities remain separated through time, as do ASRs. Generally higher survival among U.S. facilities may partly be explained by differences in regulatory oversight. Although killer whales have been housed in foreign facilities since 1964, zoo and aquarium regulation and standards in non-U.S. countries are highly variable, with some countries having little or no zoological park regulation (Cooper 2003). The captive marine mammal industry is regulated in the U.S. by the Department of Agriculture's (USDA) Animal and Plant Health Inspection Service (APHIS), which dictates requirements such as minimum facility and care specifications. Even with regulatory oversight, the USDA has apparently been unresponsive in its directive to open the rule-making process regarding how killer whales are cared for in captivity. Indeed, at the time of this writing members of the U.S. Congress were supporting an amendment to the Agriculture Appropriations bill requiring that the USDA update and enforce regulations meant to minimally protect captive killer whales in U.S. facilities.[8] In the U.S., institutions accredited by the Association of Zoos and Aquariums (AZA) are generally recognized to have committed to improving the lives of zoo animals in their care; however, despite this commitment there is still disagreement on best practices and acceptable standards among zoo professionals with regard to many captive species (Maple 2007). Meeting the sophisticated environmental, social, and nutritional demands of zoo animals such as killer whales is difficult even where effective, agreed upon conventions and standards are in place. Higher survival among killer whales held in U.S. facilities may therefore be due in part to the conditions general regulation affords them.

The KM survival curves we generated demonstrate utility in informing health surveillance and management practices by identifying points of time in captivity in which survival deteriorates given a particular cohort of whale. For instance, the survival curve of captive-born whales shows survival improvement from 1.0 to 2.0 yr of age, a notable deterioration of survival between 2.0 yr and 6.0 yr, and again between ages 11.0 yr and 12.0 yr. Given this insight, for example, managers may be advised to avoid the potentially stressful separation of captive-born calves and mothers between 2.0 and 6.0 yr of age as can happen in the transfer of whales between parks. It is interesting to note that the survival curves we generated convey both consistent and inconsistent findings from data on wild whales. For example, based on observations of northern resident (U.S.) killer whales in 1996–2004, animals aged 4.5–6.5 yr are reported to have experienced relatively high mortality (Olesiuk *et al.* 2005). Among the captive-born animals we analyzed, survival also deteriorated somewhat during this age interval. Olesiuk *et al*. (2005) also described low mortality for wild whales aged 10.5–14.5 yr, yet our analyses demonstrate a marked decline in survival during much of this age interval. This latter discrepancy suggests that advancing into physical and sexual maturity in the captive environment represents unique challenges to captive-born whales. It is known that survival of wild killer whale males, and to a lesser extent females is negatively impacted when their mothers die or are thought to be dead (Foster *et al.* 2012). Inter-park transfers of both wild-captured and captive-born killer whales are commonplace among theme park

[8]United States House of Representatives: http://huffman.house.gov/media-center/press-releases/members-of-congress-call-on-usda-to-act-to-protect-captive-orcas-and. Accessed 3 June 2014.

operators, and the practice often results in killer whale mothers being permanently separated from their offspring. Future research should attempt to better understand how survival might be affected by these separations.

We made no attempt to perform comprehensive survival comparisons between captive and wild killer whales. Killer whales are found in nearly all temperate and polar oceans globally and only a limited number of discreet wild populations have been extensively studied. Captive environments are populated, in part, by animals captured from geographically, and hence genetically segregated populations. Similarly, captive-born offspring are often crosses between animals captured from these segregated populations, or, increasingly, the offspring of crossed mothers. Therefore knowing what constitutes "normal" wild survival as a means of comparing wild killer whales with captive crosses is difficult. The analyses presented here make general comparisons to the well-studied, northern resident population of wild killer whales; however, this wild population has been under pressure for several decades by environmental contaminants, reduced prey, acoustical disturbance and other factors (Fisheries and Oceans Canada 2011). Thus, the insulted population with whom we make general comparisons may not represent the true survival potential of wild killer whales in the absence of these pressures.

Finally, known (*i.e.*, cataloged) whales are presumed deceased when missing for some period of time, yet often there is no body to confirm the death. Researchers of wild killer whales should attempt to employ KM survival analysis as a way of accounting for "lost" (*i.e.*, censored) animals. Using the techniques employed in this and other wildlife research, a clearer understanding of both captive and wild killer whale survival will continue to emerge. Results such as the survival curves presented here may help researchers better predict when killer whales will enter periods of improved or degraded survival, and how various factors may influence the relative risk of dying. Doing so should help inform and focus animal care and management practices in the captive environment, and provide a better understanding of population dynamics among wild killer whales.

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